Science of the Total Environment 639 (2018) 465–475

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Beyond classic ecological assessment: The use of functional indices to indicate fish assemblages sensitivity to human disturbance in estuaries

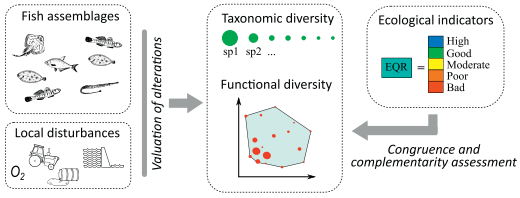
Nils Teichert *, Mario Lepage, Jérémy Lobry

Irstea, UR EABX, 50 avenue de Verdun, 33612 Cestas, France

HIGHLIGHTS

- Impact of human disturbances on fish assemblages was assessed in estuaries.
- Taxonomic and functional indices were compared to current ecological indicators.
- Local disturbances mostly affected dominant benthic species with redundant traits.
- Functional indices provide insights not reflected by taxonomic and fish indicators.
- Collapse of redundancy in impacted estuaries is a crucial concern for management.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 22 March 2018
Received in revised form 14 May 2018
Accepted 14 May 2018
Available online 26 May 2018

Editor: D. Barcelo

Keywords:
Estuary
Fish assemblage
Local disturbance
Functional traits
Functional redundancy
Ecological status

ABSTRACT

Assessing ecological health of aquatic ecosystems is crucial in the current context of biodiversity loss to guide and prioritize management actions. Although several fish-based indices were developed to assess the ecological status of estuarine ecosystems, they do not provide guidance on the causal responses of communities to disturbances. The functional trait-based approach provides an understanding of how human disturbance affects the composition of biological and ecological traits in assemblages, as well as their consequences for ecosystem functioning. Here, we evaluate the responses of fish assemblages to human disturbance in 30 French estuaries using several taxonomic and functional indices (e.g. diversity, evenness or redundancy). We tested whether these indices can provide additional information on the human impacts and health of assemblages that are not reflected by the ecological indicator (fish-based index ELFI). Results indicated that high values of local human disturbances were associated to a decrease in fish abundance, decrease in species richness and reduced functional redundancy, whereas taxonomic and functional evenness increased. In contrast, the functional richness remained stable suggesting that the functional traits of species removed by stressors were maintained by more tolerant species. Indeed, we found that the local disturbances mainly resulted in a decrease in the proportions of small benthic species feeding on macro-invertebrates, which were dominant in the studied estuaries. Some functional alterations were detected by the fish-based index, but the decline of functional redundancy was not reflected, highlighting a serious concern for management. Indeed, the abrupt collapse of functional redundancy in response to local disturbances can decrease the ability of assemblages to maintain certain species traits in the face of future environmental disturbance, including climate change. From a management perspective, the application of such functional redundancy measure in monitoring programs can help stakeholders identify sensitive areas where conservation efforts need to be planned.

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* Corresponding author.
E-mail address: nils.teichert@irstea.fr (N. Teichert).

https://doi.org/10.1016/j.scitotenv.2018.05.179
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1. Introduction

In estuarine and coastal environments, the structure and functioning of ecosystems has dramatically changed over the last century due to local human stressors, such as over-exploitation of resources, habitat fragmentation, chemical pollution or species invasions (Lotze et al., 2006). These local impacts are expected to be magnified by climate change through cumulative effects (Crain et al., 2008; Halpern et al., 2008) and specific threats (Baptista et al., 2015; Woodward et al., 2010). In this context, assessing the health and vulnerability of the ecosystem is a central concern for environmental managers who must ensure long term ecosystem functioning and avoid further degradation (Vasconcelos et al., 2017). To achieve this goal, ambitious surveillance programs have been implemented worldwide (e.g. Borja et al., 2012; Borja et al., 2008; Perez-Dominguez et al., 2012), particularly in Europe through the Water Framework Directive (WFD; 2000/60/EC). The latter requires the establishment of biotic indicators to quantify the ecological status of water bodies from several biological quality elements, from phytoplankton to fish (Hering et al., 2010; Reyjol et al., 2014). In this context, several assemblage descriptors related to species composition and ecological structure are developed to quantify the degree of biotic alteration caused by human disturbances compared to reference sites with little or no anthropogenic influence (Birk et al., 2012; Karr, 1981). The outcomes are then combined into a multimetric index to assess the health status of the assemblages (i.e. from bad to high status), which can be used as decision criteria to define conservation priorities and develop restoration measures.

In estuaries, fish and benthic invertebrate communities, as well as phytoplankton, have been increasingly monitored as valuable indicators of ecological quality because of their sensitivity to a wide range of environmental disturbances (Borja et al., 2012) and their roles in ecosystem functioning (Holmlund and Hammer, 1999) and ecosystem services (Grizzetti et al., 2016). Hence, several fish-based indices have been developed for estuaries in Europe by comparing the responses of several biological metrics to gradients of environmental degradation and combining them in multimetric indices (e.g. Lepage et al., 2016; Perez-Dominguez et al., 2012). Selected metrics generally describe the assemblage composition and abundance of specific functional guilds (e.g. ecological guild, trophic guild), so most of indices give at least partial insights into functional changes induced by human disturbances (Perez-Dominguez et al., 2012). However, direct information on the functional structure (e.g. functional diversity, evenness or redundancy) remains largely untapped in the implementation of ecological assessment (Colin et al., 2018). While multimetric indicators provide a general overview of human impact synthesized in a single score, functional approaches can provide a more integrated way of understanding the causal responses of communities to disturbances (Mouillot et al., 2013). Indeed, understanding how the composition of biological and ecological traits of species is affected by disturbance can guide conservation and management efforts (Dolbeth et al., 2016b). Moreover, by focusing on ecological traits or the role of species in ecosystem, the outcomes of functional approach may be more readily extended to the local context than taxonomic responses which are related to the biogeographical context (Colin et al., 2018).

Numerous studies emphasized the usefulness of functional approaches to detect the impact of disturbances on fish assemblages (e.g. Sagouis et al., 2016; Teresa and Casatti, 2017), including in the marine and estuarine environment (e.g. Baptista et al., 2015; Henriques et al., 2014; Selleslagh et al., 2012a; Villeger et al., 2010). For example, Dolbeth et al. (2016b) highlighted the complementarity of several indices to describe the structural and functional responses of fish assemblages to human disturbance in tropical estuaries. In such an approach to functional diversity, species traits are used to construct a multidimensional space from which several indices are calculated to convert the species distributions and abundance into functional insights (Villeger et al., 2008). These synthetic indices can thereafter be used to detect modifications in the functional structure of community in response to changes in the environmental condition or particular anthropogenic disturbances (Mouillot et al., 2013). For instance, human-induced disturbances can filter out species depending on their traits resulting in the elimination or decrease in abundance of species whose traits are sensitive to stressors. This is generally reflected in the convergence of species traits and the collapse of functional diversity (Buisson et al., 2013; Mouillot et al., 2013). This functional homogenization pattern occurs when species affected by stressors support singular functional role in the community. However, in highly redundant assemblage, the loss of sensitive species may be compensated if similar functional traits are shared by other species more tolerant to disturbances (Rosenfeld, 2002; Yachi and Loreau, 1999). In redundant coral reef fish assemblages, Brandl et al. (2016) have recently demonstrated that, while most of the functional indices do not respond, the functional originality increases when faced with an increase in habitat degradation suggesting a loss of redundancy that may increase the vulnerability of assemblage to future environmental disturbances. In such a case, the functional redundancy can play a crucial role in promoting resilience by buffering the functional alterations caused by species loss and stabilizing the functional richness (Mouillot et al., 2014).

Estuaries are transition ecosystems shaped by major environmental gradients, e.g. salinity, oxygen, depth, due to their position at the interface between marine and freshwater environments (Attrill, 2002). Therefore, fish assemblages include estuarine resident species, but they also include freshwater and marine species that typically use estuaries at a specific life stage, as well as migratory diadromous species (Potter et al., 2015). Although this variety of life history traits promotes functional diversity, the functional redundancy is generally high in estuaries compared to other continental aquatic ecosystems (Teichert et al., 2017a). The huge constraints imposed by natural environmental fluctuations, e.g. physico-chemical parameters, tidal range, limit the range of ecological strategies (Mouillot et al., 2007; Teichert et al., 2017b) and contribute to increased functional redundancy in fish communities (Dolbeth et al., 2016a; Villéger et al., 2012). Accordingly, estuarine assemblages are generally composed of few dominant species considered as stress-tolerant and well-adapted to cope with the high variability of environmental parameters. They are characterized by small and short-lived organism mainly associated with r-strategists rather than K-strategists (Gray and Elliott, 2009). In this context, the estuarine quality paradox emphasizes the difficulty of disentangling the effects of anthropogenic stress and natural constraints on biotic assemblages (Dauvin, 2007; Elliott and Quintino, 2007). Since functional properties are expected to be more stable than structural ones, functional approaches should be effective to detect the impact of human disturbance improving our understanding of how stressors affect fish assemblages (De Jonge et al., 2006). Nevertheless, taking environmental influence into account remains essential to accurately assess the effect of stressors when modeling the responses of biological indicators (Courrat et al., 2009; Sagouis et al., 2016). Indeed, van der Linden et al. (2016a) reported a predominant contribution of natural factors for to explain the functional changes in benthic assemblages of estuaries subjected to anthropogenic disturbance of the seafloor.

In this context, the present study aims to assess the impacts of human disturbances on estuarine fish assemblages based on a comparative analysis of taxonomic and functional indices. We then tested whether these indices can provide additional information on the effects of human impacts and on assemblage health that were not already integrated into current ecological quality indicators. Specifically, we used a database of 30 French estuaries (period 2006–2016) to describe and quantify the responses of fish assemblages to a local human disturbance gradient, taking into account the influence of environmental variables. We then assessed the capacity of the current fish-based index (Estuarine and Lagoon Fish Index, ELFI) used in the WFD to detect and reflect the functional alterations of fish assemblages (Delpech et al., 2010). We expected functional approaches to provide additional insights about

health status of fish assemblage because of their ability to reveal the causal responses of communities to disturbance, which are influenced by species' traits. These results have important implications for management and implementation of ecological monitoring, particularly for assessing the functional sensitivity of assemblages.

2. Materials and methods

2.1. Estuarine attributes

Fish were sampled in 30 estuaries along the French Northeast Atlantic coast (Fig. 1). For each estuary, the environmental conditions were described using eleven variables (nine continuous and two categorical variables) related to geomorphological and hydrological attributes influencing fish assemblages in estuaries (Table 1). Data used were obtained from institutional reports and previously published data (Nicolas et al., 2010b). Continuous variables related to the size of the system have been log-transformed to reduce the influence of the few larger systems on the smaller ones. An additional variable reflecting the intensity of local human disturbance on the estuarine ecosystem was included using the cumulative pressure index proposed by Lepage et al. (2016). Such a global index was preferred because the number of sites was not sufficient to disentangle the unique contribution of several stressors. The pressure index included eight metrics reflecting the main categories of estuarine disturbance: 1-intertidal area lost, 2-interference with the hydrographical regime, 3-anthropogenically affected coastline, 4-water chemical quality, 5-water quality biological effects, 6-benthos status, 7-dissolved oxygen in time and 8-dissolved oxygen in space. Each metric was assigned a score between 0 and 9 depending on the severity of the disturbance (see Lepage et al. (2016) for more details on standardized thresholds criteria used for each metric). Finally, the disturbance index was calculated as the sum of all metric scores and can range between 0 (no disturbance) to 72 (very high disturbance).

Table 1
Environmental variables and disturbance index used to describe the estuaries along the French coast. Asterisks indicate variables removed from analysis due to their strong collinearity (Spearman coefficient > 0.7).

Environmental descriptors	Ranges and units or classes
Continuous variables	
Latitude	43.37–50.23 °
Mean annual river discharge	1.22–960.00 $m^3 \cdot s^{-1}$
Watershed area*	75–117,955 km^2
Estuary area	1.5–532.9 km^2
Estuary length*	7.0–170.9 km
Entrance width*	0.18–16.00 km
Entrance depth	5.0–20.0 m
Tidal range*	3.0–11.8 m
Intertidal area	0.75–83.5%
Disturbance index	7–54
Categorical variables	
Turbidity	Low (<200 NTU); high (≥200 NTU)
Dominant substrate	Mud; mud-sand; sand-gravel; mixed sediment

2.2. Fish surveys

Fish data were collected within the WFD monitoring program conducted between 2006 and 2016. During this period, estuaries were sampled in spring and autumn during two or three years. For each survey (i.e., one estuary, one year, one season), fish were sampled using a beam trawl (1.5 or 3 m large, 16–20 mm mesh size) in application of the standard French protocol (AFNOR, 2011; Delpech et al., 2010). For each survey, sampling was stratified by salinity zones, i.e. oligohaline (salinity <5), mesohaline (salinity between 5 and 18) and polyhaline (salinity >18) zones. A minimum of eight samples was collected from each salinity zone along the whole upstream-downstream gradient of estuaries. The total number of samples per survey varied between 8 and 78, essentially depending on the estuary size. For each sample, the beam trawl was towed for 15 (14.7 ± 2.5) minutes at a speed of 1.5 to

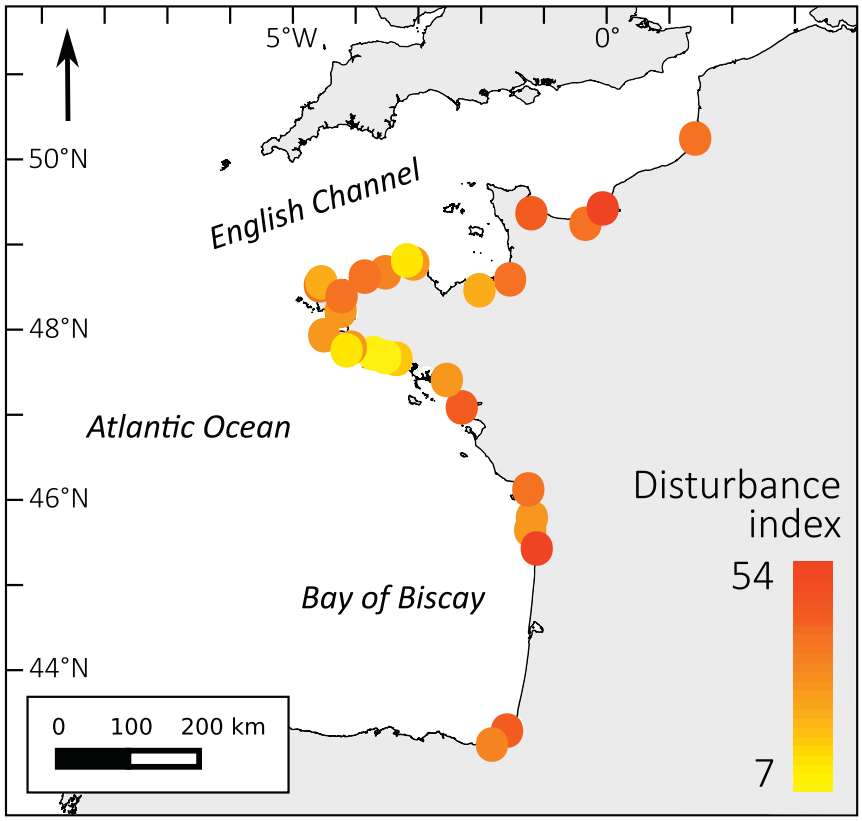

Fig. 1. Spatial distribution of the 30 estuaries along the French coast, North East Atlantic. Color levels indicate the intensity of human disturbance for each estuary.

3 knots. A total of 165 surveys spanning 3552 samples were carried out in the 30 estuaries. All captured fish were identified to the species level and measured to the nearest millimetre (TL, mm). In the case of very abundant species, only the lengths of a sub-sample of 30 individuals were recorded. Abundances of all fish species were then expressed in number of individuals per 1000 m^2 trawled.

2.3. Fish-based multimetric index

For each survey, the ecological status was assessed by calculating ELFI (Delpech et al., 2010), which is currently used for determining the ecological status of French transitional waters for the needs of WFD. This multimetric index is composed of seven metrics related to the species composition and the abundance of several functional guilds in the estuarine assemblages. The metrics were selected because of their effective response to human disturbances (Delpech et al., 2010) and included species richness, total fish abundance, and abundance of diadromous, marine juvenile, estuarine resident, freshwater, as well as benthic species (Lepage et al., 2016). Following ELFI method, a score, ranging from 0 to 4, was attributed to each metric according to standardized threshold values taking into account spatiotemporal conditions of sampling and estuarine characteristics, namely the ecoregion, the size of estuary, salinity and season. The scores were then combined for each survey to obtain an Ecological Quality Ratio (EQR), which ranges from zero to one. Finally, one of five quality classes or status (high, good, moderate, poor, bad) was assigned to the survey, where EQR values close to zero indicate "bad" status and EQR values close to one indicate "high" status. The boundary values of ecological classes for ELFI method were defined during an intercalibration process and harmonized with the different fish classification methods used for the WFD assessments of transitional waters in the Northeast Atlantic region (Lepage et al., 2016).

2.4. Taxonomic and functional indices

The diversity and structure of fish assemblages within surveys were assessed using a set of four taxonomic and eight functional indices (Table 2). While taxonomic indices consider all species as equally distinct (Magurran, 2004), the functional indices integrate information on species traits to determine their proximity in a multidimensional functional space (Villeger et al., 2008). Here, the functional niches of species have been described using four biological traits commonly used to reflect habitat preference and trophic position of species in estuaries, i.e. body size, diet, salinity preference and position in the water column (see Henriques et al., 2017 for detailed explanations of species traits and their relevance). Fish traits were obtained from Teichert et al. (2018) that investigated patterns of functional diversity for the same set of estuaries. The fish body size was coded using four ordered categories, i.e. < 8],]8;15],]15;30] and > 30 cm. The dominant food item in their diet was coded according to six categories, i.e. piscivorous, omnivorous, planktivorous, herbivorous, benthic invertebrate feeder, and supra-benthic invertebrate feeder. Salinity preference was coded using four categories, i.e. marine, brackish, freshwater, and diadromous species. Finally, the position in the water column was expressed in three categories, i.e. pelagic, demersal, and benthic.

To calculate the functional indices, the pairwise functional distances between species were firstly computed using the Gower's distance metric (Gower, 1971). These distances were then used to perform a principal coordinate analysis (PCoA), which produces an Euclidean space where species are ordered depending on their trait values. The first five PCoA axes were chosen to construct a multidimensional functional space (Mouillot et al., 2013) because this threshold provide satisfactory trade-off between the minimum species number in assemblages and the quality of functional space (Maire et al., 2015). Indeed, the pairwise distances obtained from this five dimensional space remained highly correlated with the initial Gower matrix (Mantel test, $r = 0.93$, $P < 0.001$).

Taxonomic and functional indices were calculated at the survey scale by pooling available samples. Therefore, a resampling procedure was performed to account for the sensitivity to sampling effort of the diversity measures. For each survey, indices were calculated on a basis of eight samples (minimum number of samples per survey) randomly selected from the total number of samples. This resampling was repeated 100 times and average values were used to obtain rarified values of taxonomic and functional indices.

2.5. Statistical analyses

Responses of taxonomic and functional indices to human disturbance were quantified using linear mixed models (LMMs). LMMs were adjusted with fish indices as response variables, while season, environmental variables and disturbance index were used as explanatory variables. Estuary was included as a random effect to account for multiple-year samplings and models were adjusted using an identity link function and a Gaussian error distribution. Environmental predictors were included in the models to account for the influence of others

Table 2
Summary of the taxonomic and functional indices used to investigate changes in estuarine fish assemblages in response to human disturbance. The description of indices is provided with the abbreviation (Abbrev.) used in the manuscript. We specified if the indices calculation include information on species abundances (Abund.)

Names	Abbrev.	Description	Abund.	References
Taxonomic indices				
Total abundance	*Abund*	Total abundance of species in the assemblage	Yes	/
Species richness	*Rich*	Total number of species in the assemblage	No	Magurran (2004)
Simpson diversity	*Simp*	Probability that two individuals randomly selected in the assemblage belong to different species	Yes	Ricotta et al. (2016)
Pielou evenness	*Pielou*	Evenness of species abundances in the assemblage	Yes	Magurran (2004)
Functional indices				
Functional richness	*FRic*	Proportional volume of the functional space filled by species of the assemblage	No	Villeger et al. (2008)
Functional diversity	*Rao*	Abundance-weighted sum of pairwise functional distances between species (Rao's Quadratic Entropy)	Yes	Ricotta et al. (2016)
Functional evenness	*FEve*	Abundance-weighted regularity of species in the functional space along the shortest minimum spanning tree	Yes	Villeger et al. (2008)
Functional divergence	*FDiv*	Proportion of the total abundance that is supported by the species with the most extreme functional traits	Yes	Villeger et al. (2008)
Functional dispersion	*FDis*	Abundance-weighted mean distance of species from the center of the assemblage in the functional space	Yes	Laliberte and Legendre (2010)
Functional redundancy	*Redun*	Abundance-weighted functional redundancy, i.e. 1 - (Rao/Simp)	Yes	Ricotta et al. (2016)
Functional specialization	*FSpe*	Abundance-weighted mean distance of species from the center of the functional space	Yes	Mouillot et al. (2013)
Functional originality	*FOri*	Abundance-weighted mean pairwise distance between a species and its nearest neighbor species in the functional space	Yes	Mouillot et al. (2013)

abiotic factors than human disturbance. To limit multicollinearity and redundancy between the explanatory variables, four variables were excluded from the analyses because their correlations exceeded 0.7 with other variables (Table 1), as estimated from the Spearman coefficients (Supplementary material, Table S1). The responses variables were square-roots-transformed to meet assumptions of normality, with the exception of abundance data which was log(x + 1)-transformed. Both response and predictor variables were standardized following the method proposed by Gelman (2008), so that the magnitudes of model coefficients can be directly compared as effect sizes. A multi-models inference approach was used to evaluate the importance of each predictor and to obtain model-averaged results, which provides more stable estimates than those using a single model (Grueber et al., 2011). For each response variable, all possible models were fitted, ranked according to their AIC_C value (Akaike's Information Criterion corrected by sample size), and the top two of the models based on AIC_C (thereafter top $2AIC_C$) were used to calculate averaged coefficients and confidence intervals. There is evidence that the predictor variables significantly affect the response variable if confidence intervals do not include zero (Grueber et al., 2011). The relative importance of predictors, ranging between 0 and 1, was assessed using the sum of Akaike evidence weights. In such approach, the 0.8 threshold is commonly used to identify the explanatory variables that significantly contribute to explain variation of the response (Calcagno and de Mazancourt, 2010). The proportion of deviance explained by the LMMs was assessed using the marginal R^2_m (variance explained by the fixed effects) and the conditional R^2_c (variance explained by both the fixed and random effects; Nakagawa and Schielzeth, 2013). To assess the robustness of the results, a hierarchical partitioning analysis was conducted to determine the independent contribution of the predictors to explain the taxonomic and functional indices. This method deals with the collinearity bias by decomposing variation of each predictor in a unique and conjoint contributions with all other variables (Nally and Walsh, 2004). The significance of models was then assessed using randomized permutation tests for hierarchical partitioning.

To support our interpretation of changes in the functional structure of assemblages, additional LMMs were adjusted to determine the individual responses of fish functional traits along the disturbance gradient. The models were implemented by following an approach similar to that previously detailed for the diversity indices, but using the relative proportions of each trait category as response variables. These proportions were determined for the four biological traits i.e. body size, diet, salinity preference and position in the water column, by calculating the percentage of fish assigned to the categories in the surveys.

Finally, the relationships between EQR, taxonomic and functional indices were investigated using a non-metric multidimensional scaling (NMDS) and a Permanova was performed to test for differences between ecological statuses (high, good, moderate, poor, and bad). Both methods were conducted using Euclidian distance as dissimilarity index and fish indices as input matrix. The statistical threshold was established at $P < 0.05$. Then, Spearman rank correlation coefficients were used to determine the strength of the relationships between the EQR values determined from ELFI and the taxonomic and functional indices. This analysis assessed the ability of ELFI to reflect changes in taxonomic and functional structure of fish assemblages.

Analyses were performed in the R environment (R Core Team, 2012) using the package "*vegan*" (Oksanen et al., 2015) for calculating taxonomic indices and the functions "*multidimFD*" and "*uniqueness*", respectively provided by S. Villeger (available online at http://villeger.sebastien.free.fr) and Ricotta et al. (2016), for calculating functional indices. ELFI was calculated using an ad hoc function coded in R. The LMMs were fitted using the package "*lme4*" (Bates et al., 2014). The multi-models inference approach was conducted using the package "*MuMIn*" (Bartoń, 2013), variables were standardized using the package "*arm*" (Gelman and Su, 2015) and the hierarchical partitioning analysis was conducted using the package "*hier.part*" (Walsh et al., 2003). Finally, the NMDS was performed using the function "*metaMDS*" and indices were projected onto ordination using the function "*envfit*" of the package "*vegan*" (Oksanen et al., 2015).

3. Results

3.1. Responses of taxonomic and functional indices

The total proportion of deviance explained by the LMMs varied according to the different fish indices, R^2_c ranging from 0.25 and 0.67, but the contribution of fixed predictors taken separately was lower (R^2_m ranging from 0.07 to 0.45). The important contribution of the random effect (i.e. estuary) suggests the involvement of sources of variability related to estuaries features that were not reflected by fixed predictors. Overall, the explanatory power of fixed predictors was variable among the taxonomic indices (R^2_c ranging from 0.10 to 0.45), with the highest values recorded for total abundance and species richness (Table 3). Similarly, R^2_c values varied from 0.07 to 0.40 for taxonomic indices, with the highest values recorded for the functional diversity and redundancy. The relative importance of predictors indicated that indices have obviously fluctuated between the spring and autumn periods, with the exception of functional richness (*FRic*), functional eveness (*FEve*) and functional redundancy (*Redun*). Most of the environmental variables were included in the top $2AIC_C$ of models, which confirms the usefulness of controlling for their effects to disentangle the responses of fish indices to human disturbances. The relative importance of environmental factors was highly variable depending on indices (Table 3), but the substratum composition had a predominant effect on seven indices, followed by the estuary surface and entrance depth (relative importance >0.8 for three indices). The individual effect of environmental variables has not been described here, but a detailed summary of model coefficients is provided in Tables S2. Overall, the unique contributions of predictors determined from the hierarchical partitioning analysis revealed similar trends, especially in regards to the impact of human disturbance (Table S3).

According to the LMMs, the relative importance of the disturbance index was higher than 0.8 for seven indices (Table 3) and the confidence intervals for their standardized coefficients did not crossed zero, revealing a significant influence of human disturbances (Fig. 2). Functional redundancy, species richness and total abundance were significantly reduced when the disturbance index increased, while taxonomic and functional evenness showed an inverse trend, as well as functional dispersion and diversity. These results suggest that human disturbances caused the removal and decline in abundance of species that are mostly redundant in assemblages, resulting in higher regularity in species abundance distributions and functional traits. In contrast, there was no evidence that Simpson's diversity index, functional specialization and functional originality significantly changed with the intensity of human disturbance. In addition, the disturbance index was not included as explanatory variable in the top 2AICc of models adjusted for the functional richness and divergence, indicating that these indices were more related to environmental variables than human disturbances.

3.2. Responses of functional groups

The most abundant species in the surveys were *Pomatoschistus minutus* and *Pomatoschistus microps*, followed by *Sprattus sprattus*, *Gobius niger*, *Solea solea* and *Platichthys flesus*. Therefore, fish assemblages were dominated by small size species (<8 cm) living preferentially in brackish environment (Fig. 3). Similarly, the benthic species feeding on invertebrates represented the largest amount of fish abundance, whereas other trophic groups were more rare, especially the piscivorous and herbivorous species.

According to LMMs, the proportions of deviance explained by the fixed predictors (r^2m) varied between 0.03 and 0.33, but the conditional coefficients of determination were higher (r^2c ranging between 0.14

Table 3
Relative importance of the nine explanatory variables, including season and disturbance index, estimated using the multi-models inference approach for the taxonomic and functional indices. The importance values range between 0 and 1, where values close to one indicate higher importance of the variable. The number of models included in the top $2AIC_C$ was specified, along with the marginal (r^2m) and conditional (r^2c) coefficients of determination. The dashes indicate explanatory variables not included top $2AIC_C$ of models. Values in bold indicates importance >0.8.

Fish index	Disturbance index	Season	Latitude	River discharge	Estuary area	Entrance depth	Intertidal area	Turbidity	Substratum composition	Number of models	R^2m	R^2c
Abund	**1.00**	**1.00**	0.21	–	–	**1.00**	0.77	0.21	**1.00**	4/255	0.45	0.67
Rich	**1.00**	**1.00**	0.10	0.15	0.22	0.79	0.10	0.09	**0.90**	7/256	0.35	0.65
Simp	0.10	**1.00**	0.09	0.20	0.65	–	0.09	0.57	–	8/256	0.10	0.25
Pielou	**1.00**	**1.00**	0.29	0.14	**1.00**	0.66	0.15	0.43	–	12/256	0.21	0.39
FRic	–	0.33	–	0.41	0.33	0.78	0.23	0.62	**1.00**	17/256	0.24	0.44
Rao	**1.00**	**1.00**	0.13	0.28	**1.00**	0.73	**1.00**	**1.00**	**1.00**	4/256	0.33	0.41
FEve	**1.00**	0.18	0.20	0.18	–	**1.00**	**1.00**	–	**1.00**	4/256	0.21	0.30
FDiv	–	**1.00**	0.22	0.08	0.24	0.56	–	0.42	–	11/256	0.13	0.45
FDis	**1.00**	**1.00**	–	0.23	**1.00**	0.45	0.69	**1.00**	**0.90**	7/256	0.27	0.36
Redun	**1.00**	0.45	–	0.10	0.05	**0.90**	0.49	0.38	**1.00**	13/256	0.40	0.64
FSpe	0.06	**1.00**	0.06	0.27	0.15	0.08	0.15	0.50	–	11/256	0.07	0.59
FOri	0.10	**1.00**	–	0.65	0.65	0.34	–	0.55	–	8/256	0.12	0.43

and 0.79), similarly to those obtained for the taxonomic and functional indices. The sensitivity of fish traits to disturbance was quantified while taking into account the influence of environmental variables (the importance of predictors and coefficients are provided in Table S4 and S5). As reported for the functional indices, the relative importance of environmental factors has fluctuated depending on the species traits (Table S4), with traits categories related to salinity preference and trophic regime being commonly related to several natural parameters. In general, the small sizes species tended to be more sensitive to human disturbance, which increases the relative proportion of large fish in impacted estuaries (Fig. 3a). Although non-significant, the proportion of brackish species was lower in disturbed estuaries, whereas the contribution of freshwater species increased (Fig. 3b). The proportion of benthic species in fish assemblages was significantly reduced for high levels of human disturbances, resulting in higher contributions of demersal and pelagic species (Fig. 3c). This trend was also reflected by the trophic groups, indicating that the proportion of benthic invertebrate feeders decreased with increasing disturbance intensity, and that the proportion of supra-benthic invertebrate feeders increased mechanically (Fig. 3d).

3.3. Fish-based index, taxonomic and functional indices

Our results confirmed that the ELFI index was able to detect the impact of human disturbances, as revealed by the negative correlation between EQR and the disturbance index (Spearman correlation test, $n = 165$, $r = -0.41$, $P < 0.001$). The two-dimensional NMDS performed on EQR, taxonomic indices, and functional indices reached a stress value of 0.14 indicating an acceptable adjustment of the ordination. The projection of the different fish indices revealed a strong association between *Pielou*, *Simp*, *FOri*, *FDis* and *Rao* which were inversely related to *Redun*, *FSpe* and *FDiv* (Fig. 4). This suggested that the functional redundancy and functional specialization of fish assemblages tended to decrease when abundances of both species and traits, were more evenly distributed. On the other hand, species richness and functional richness (*Rich* and *FRic*) were inversely related to *FEve* (Fig. 4). Interestingly, ELFI was primarily related to total fish abundance (*Abund*) and the richness-based indices, resulting in significant differences between ecological status, i.e. high, good, moderate, poor, and bad (Permanova, $n = 163$, $r^2 = 0.30$, $P < 0.001$). Accordingly, higher ecological status was generally associated with high abundance and high levels of species richness and functional richness, but with a low degree of functional evenness (Fig. 4).

These results were supported by the correlation analysis, revealing that eight of the twelve indices were significantly associated to the EQR values determined from ELFI (Table 4). Some indices were positively related to ELFI, such as *Abund*, *Rich*, *FRic*, and *FDiv*, whereas others revealed negative trends, i.e. *Pielou*, *FEve* and *FOri*. These results support the previous statements that fish assemblages assigned to high ecological status view through ELFI usually displayed low level of taxonomic and functional evenness, despite high values of taxonomic and functional richness. Note that the changes in *FOri* highlighted that the functional distance between nearest neighbor species tend to decrease when the ecological status of assemblages is enhanced. Finally, *Simp*, *Rao*, *FDis*, *Redun* and *FSpe* were not significantly correlated with the EQR values, highlighting that such taxonomic and functional information were not incorporated and thus reflected by ELFI.

4. Discussion

Our results demonstrated the impacts of local human disturbances on the taxonomic and functional structure of fish assemblages in estuaries, while taking into consideration the influence of environmental factors. Overall, fish abundance, species richness, functional richness and

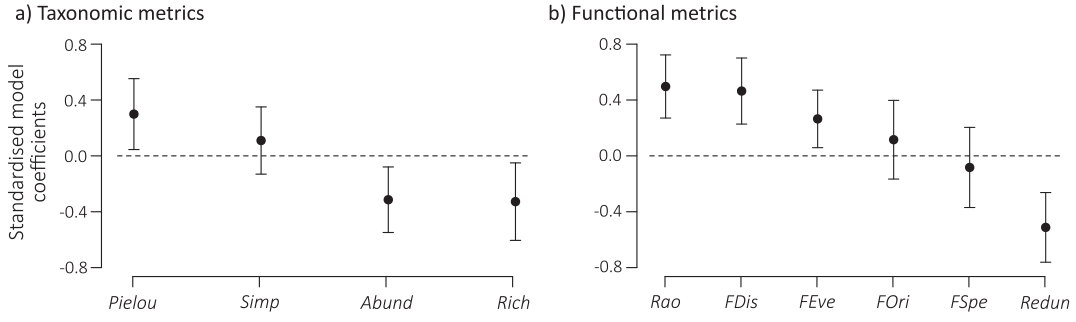

Fig. 2. Effect of local human disturbance on a) taxonomic and b) functional indices of fish assemblages, as estimated by the standardized coefficients of linear mixed models. The vertical bars represent the 95% confidence intervals. There is evidence that human disturbance significantly influence the indices when the confidence interval does not include zero. Functional richness and functional divergence are not presented because disturbance was not selected as explanatory variable in the top 2AICc of models. The meaning of abbreviations is provided in Table 2.

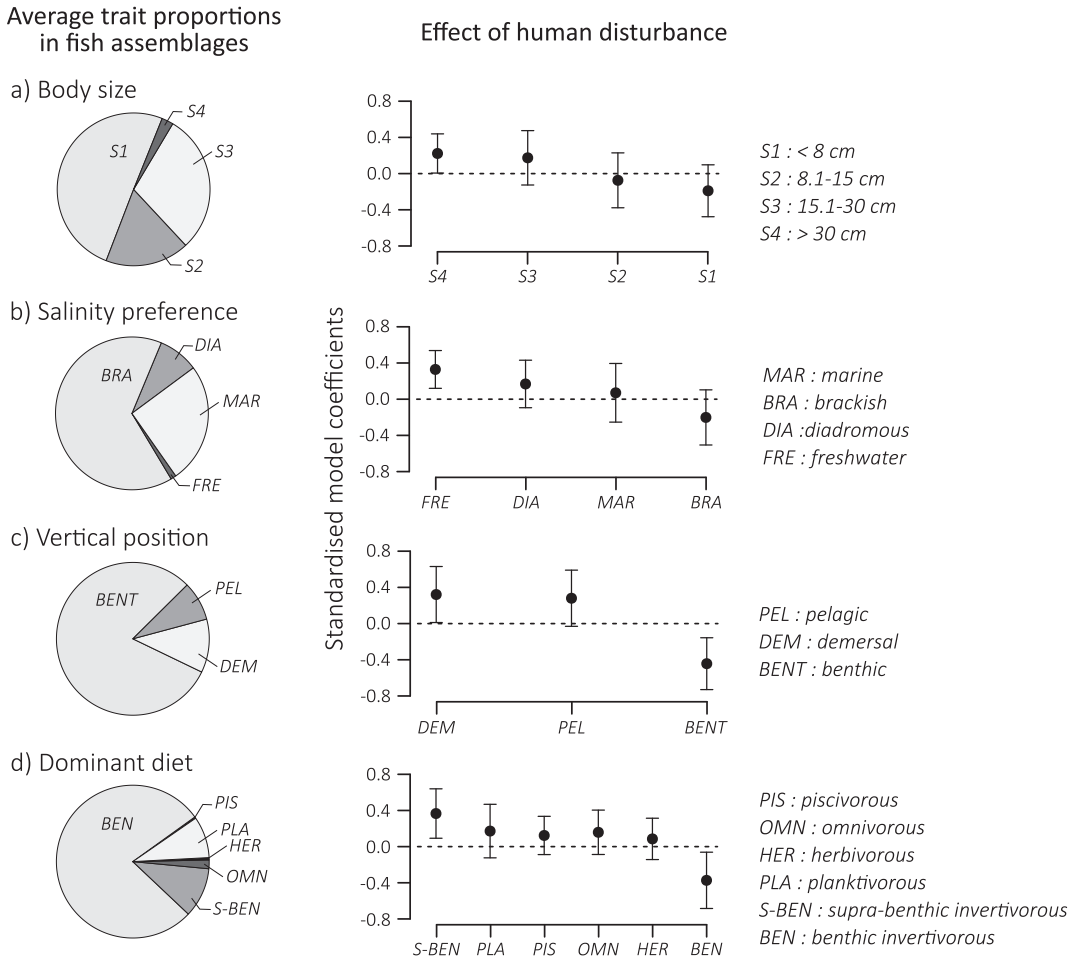

Fig. 3. Proportion of fish trait categories in estuarine fish assemblages and effect of local human disturbance on a) body size, b) salinity preference, c) vertical position and d) dominant diet. The pies charts indicate the average proportions of each category recorded in fish assemblages. The graphs on the right side show the standardized coefficients of the human disturbance index estimated by linear mixed models for each functional traits category. The vertical bars represent the 95% confidence intervals. There is evidence that human disturbance significantly influence indices when the confidence interval does not include zero.

redundancy decline when assemblages faced with stressors, whereas taxonomic and functional evenness increased. These changes, caused by variations in functional traits proportions, were only partially reflected by ELFI and deserve additional attention to improve the environmental monitoring of estuaries.

4.1. Responses of taxonomic and functional indices

Modifications of natural conditions can cause important changes in the taxonomic and functional structure of fish assemblages in aquatic environments, including marine (e.g. Brandl et al., 2016; D'agata et al.,

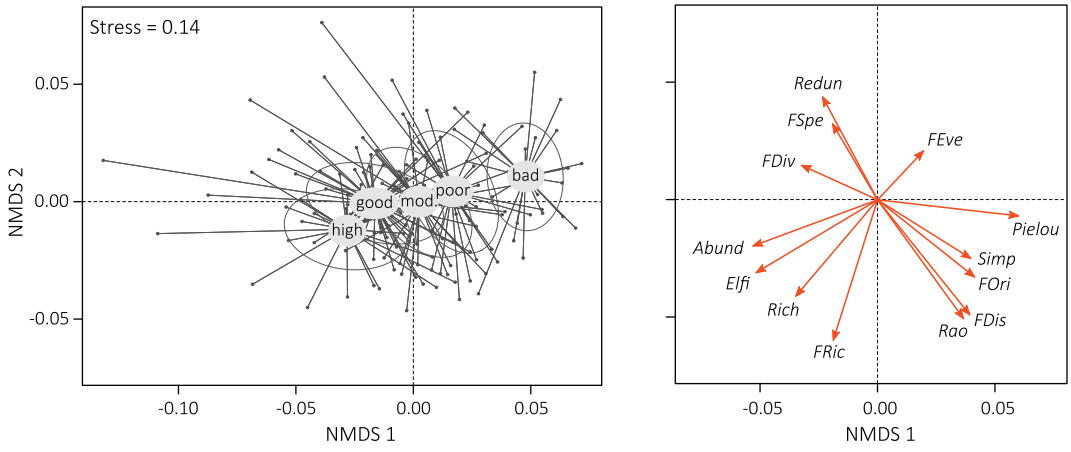

Fig. 4. Relationships between fish-based index, taxonomic and functional indices seen by a two-dimensional NMDS ordination. The left panel presents the projections of surveys (points) according to the ecological status categories determined from the ELFI fish-based index, i.e. bad, poor, moderate, good and high. The right panel presents the projections of fish indices (arrows). The meaning of abbreviations is provided in Table 2.

Table 4
Spearman correlation coefficients (rho) between the EQR values determined from the ELFI fish-based index and the taxonomic and functional indices. Mean and range of indices are provided. Values in bold indicate $P < 0.05$.

			Correlation with ELFI	
Fish index	Mean	Min-Max	rho	*P*-value
Abundance	63.4	0.42–651.10	0.88	< **0.001**
Species richness	13.85	2.46–24.95	0.58	< **0.001**
Simpson diversity	0.63	0.13–0.86	−0.07	0.999
Pielou evenness	0.57	0.12–0.94	−0.37	< **0.001**
Functional richness	0.03	0.00–0.11	0.43	< **0.001**
Functional diversity	0.29	0.03–0.53	−0.18	0.265
Functional evenness	0.45	0.17–0.70	−0.42	< **0.001**
Functional divergence	0.91	0.72–0.99	0.32	< **0.001**
Functional dispersion	0.45	0.04–0.80	−0.17	0.334
Functional redundancy	0.54	0.24–0.88	0.17	0.321
Functional specialization	0.65	0.53–0.79	0.18	0.239
Functional originality	0.10	0.00–0.37	−0.26	**0.010**

2016), freshwater (e.g. Sagouis et al., 2016; Teresa and Casatti, 2017) and estuarine ecosystems (Villeger et al., 2010). The ability of taxonomic and functional indices to detect assemblage alterations remains highly dependent on the regional context (Teresa and Casatti, 2017), the taxonomic composition (van der Linden et al., 2016b) and the targeted source of disturbance (van der Linden et al., 2016a). Here, the LMMs adjustments have varied according to the fish indices (R^2_c ranging between 0.25 and 0.65), with a large proportion of deviance that remained not explained by the fixed predictors. This is a common feature for estuarine fish data that are subjected to stochastic processes, including a large temporal variability in fish abundance (Selleslagh et al., 2012b). As a result, the performances of our models were consistent with other studies using similar analyses to investigate species distributions (e.g. França and Cabral, 2016) or assemblage compositions in estuaries (e.g. França and Cabral, 2015; Nicolas et al., 2010a; Teichert et al., 2018). In estuaries, the taxonomic and functional structures of fish assemblages are known to be influenced by regional and local conditions (e.g. Henriques et al., 2017; Teichert et al., 2018). In this study, most fish indices were related to substratum composition, entrance depth, estuary area and intertidal area, which are known to influence fish resource availability and connectivity with the marine environment (Henriques et al., 2017; Selleslagh et al., 2009). Therefore, taking into account the effects of environmental variables is essential to assess sensitivity of fish indices to human disturbances. LMMs and hierarchical partitioning analyses revealed similar trends, emphasizing a significant impact of human disturbances on fish abundance, species richness, taxonomic and functional evenness, functional diversity, dispersion and redundancy. In contrast, taxonomic diversity, functional divergence, specialization and originality were not affected but primarily associated to environmental variables.

In general, the intensification of local disturbances is associated to a decline in species richness and a reduction in fish abundance in the assemblages. Similar negative trends were reported by several studies on fish (e.g. Courrat et al., 2009; Rochette et al., 2010) and macroinvertebrates (e.g. Powers et al., 2005) in estuaries, stressing a decline of biodiversity and a reduction of carrying capacities in impacted areas. Interestingly, despite the correlation between species richness and functional richness, the intensity of disturbances was not significantly related to change in functional richness. This result suggests that the functional roles of species removed by stressors are ensured in assemblages by other species. The sharp decrease in functional redundancy when assemblages faced disturbances confirms this claim and highlighted that species loss and abundance decline were mainly concentrated on dominant and redundant functional groups. Similar results were reported in coral reef fish assemblages, where the functional originality increased after extreme weather events due to the decline of functionally redundant species sensitives to habitat degradation (Brandl et al., 2016). In estuarine environment, Dolbeth et al. (2013) also found a decline in functional redundancy of macroinvertebrate communities during eutrophication-disturbance periods.

Examination of functional trait categories indicated that anthropogenic disturbances primarily caused a drop in the relative proportions of small benthic species associated to estuarine conditions feeding on macro-invertebrates. Species supporting these functional traits (e.g. *P. minutus, P. microps*, *G. niger*, *S. solea* or *P. flesus*) were generally dominant in assemblages, so that reducing the abundances of these species favoured higher taxonomic and functional regularities. This mechanistic process was reflected by the indices of taxonomic evenness and functional evenness, indicating more balanced distributions in species abundances and functional traits when the intensity of stressors increased. The same process can explain the positive relationships of the disturbance index with functional diversity and dispersion, which are highly correlated due to their similar conceptual basis (Laliberte and Legendre, 2010). The values of these two indices increase with the functional dissimilarity and the abundance regularity between species that compose the fish assemblages. Therefore, an unexpected property is that exclusion of redundant species or decline of dominant species can lead to higher diversity values, resulting in counter-intuitive outcomes (Cooper et al., 2008; Ricotta et al., 2016). According to our results, such a pattern can occur in estuaries when fish assemblages face human disturbance. Even if responsive to anthropogenic alterations, these two indices should be applied with caution and additional indices (e.g. richness, evenness, individual traits information) are required to support a robust interpretation of functional diversity. On the other hand, Simpson's diversity, functional divergence, originality and specialization did not vary significantly with the disturbance index. This underlines the importance of using a wide range of complementary indices to accurately detect and describe the changes in fish assemblages caused by human disturbance (Mouillot et al., 2013). Borja et al. (2011) reported similar results for benthic indices in transitional waters, highlighting some inconsistencies between indicator responses to anthropogenic pressure gradients. Although the common taxonomic indices may have indicated a change in assemblage composition, the functional indices provide insights on the causal responses of assemblages based on species traits.

Our results indicated that the human-induced disturbances mainly affected fish species of the benthic compartment, which appeared sensitive to stressors despite their high abundance. Loss and degradation of critical habitats may result in a sharp decline in local abundances and biomasses of benthic species, as it was demonstrated for fish that use coastal areas as nursery ground (Bilkovic, 2011; Rochette et al., 2010). Similarly, Courrat et al. (2009) reported that the estuaries nursery function may be disturbed by changes in water quality due to pollution by heavy metals and organic contaminants. Dredging activities can also induce significant changes in the demersal fish assemblage structure, including compositional changes and diversity loss (Barletta et al., 2016; Uriarte and Borja, 2009). Moreover, the repeated periods of oxygen depletion reported for several estuaries can have severe consequences on benthic fish fauna (Baden et al., 1990), including direct mortality, physiological and/or behavioral stress, or a drastic reduction of macroinvertebrates that are preys to fish (Powers et al., 2005). Beyond this non-exhaustive list of threats (Vasconcelos et al., 2007), the sensitivity of benthic species in estuaries can also be explained by their life histories. Most of the small benthic species feeding on invertebrates were resident fish associated to brackish conditions (e.g. *Pomatochistus* sp.) or marine juveniles fish living in estuaries for several years (e.g. *Solea* sp.). These species are exposed to the estuarine conditions, and thus local anthropogenic stress, for a potentially long period of time and during early life stages, which are known to be highly sensitive to environmental disturbances (Ramos et al., 2012). As a result, environmental monitoring programs should pay a specific attention to small benthic species that may be severely impacted by human disturbance in estuaries and that could act as an early warning in case of further anthropogenic disturbance.

4.2. Ecological status and insights of functional assessment

Fish-based indices are designed for responding to anthropogenic stress (Perez-Dominguez et al., 2012), allowing to identify areas that should be considered for conservation or restoration actions (Borja et al., 2012). Our results confirmed that ELFI was able to detect the impact of human disturbances on fish assemblages in estuaries (Delpech et al., 2010; Lepage et al., 2016). Variations in ELFI were essentially related to changes in fish abundance, species richness and functional richness, which is consistent with the structure of a multimetric index integrating information on species richness and abundances of several functional guilds (Delpech et al., 2010). In summary, the more functional guilds show high abundance and high diversity, the better is the ecological status. Based on our results, the variations in taxonomic indices according to the EQR values determined from ELFI were consistent with the expected responses to human disturbance. However, although ELFI incorporates some information on species traits, it only offers a partial view of the functional alterations. For instance, the decrease of functional evenness with increasing disturbance intensity was reflected by ELFI, but changes in functional diversity and dispersion were not. Similarly, although a strong negative relationship is expected between human disturbance and redundancy, this pattern has not been reflected by ELFI. Nevertheless, note that the functional originality, representing the functional distance between nearest neighbors, is reduced for the higher ecological status, suggesting a greater functional redundancy in fish assemblages.

Functional redundancy is a widespread property in estuaries, where environmental constraints limit the range of ecological strategies through a convergence of species' life-history traits and feeding habits (Baptista et al., 2015; Dolbeth et al., 2016a; Teichert et al., 2017b), so that several species distributed along the estuaries share similar functional attributes (Villéger et al., 2012). Accordingly, estuarine fish assemblages are expected to be more functionally buffered against species extinction than freshwater ecosystems (Teichert et al., 2017a). Indeed, functional redundancy can play a crucial role in maintaining post-disturbance ecosystem processes, because functional traits of sensitive species can be supported by other species more tolerant to environmental stress (Naeem, 1998; Yachi and Loreau, 1999). According to our results, such compensatory process likely occurred in estuaries, as indicated by the stability of functional richness despite significant species loss. However, our results also demonstrated substantial changes in the composition of functional traits within assemblages, especially leading to higher functional evenness and lower redundancy in impacted estuaries. This demonstrates that local disturbances contribute to increase the functional sensitivity of fish assemblages that become less buffered against species loss (Fig. 5). In this context, additional disturbances can produce important alterations of ecosystem functioning since most of functional traits remain supported by non-redundant species (Micheli and Halpern, 2005). This is a major concern in the perspective of climate change which should amplify current threats and cause specific disturbances, such as alterations in temperature regimes or an increase in the frequency and intensity of droughts and extreme flow events (Milly et al., 2005; Woodward et al., 2010). Maintaining high diversity and redundancy in functional traits is thus a critical management perspective to improve the chances of biological assemblages to accommodate future environmental changes.

From an applied perspective, the current ecological assessment based on the fish-based indices appeared efficient in detecting estuaries impacted by human disturbance. However, ELFI did not accurately reflect the functional alterations in fish assemblages caused by environmental disturbance. Our results suggest that functional redundancy assessment can provide complementary information for determining the compensatory potential of assemblages contributing to ecosystem resilience (Mouillot et al., 2014). Integrating such redundancy measures into monitoring programs is of interest to identify the sensitivity of local assemblages and to prioritize management actions to avoid further alteration of biodiversity or severe degradation of ecosystems (Parravicini et al., 2014; Teichert et al., 2017a). The decline in functional redundancy should be a central concern for estuary management because it denotes a decrease in the ability to maintain certain functions in the face of future threats. In such a scenario the arrival of additional disturbance may result in the decline or extinction of species supporting singular functional traits (Fig. 5), leading to the collapse of functional richness and ecosystem functioning (Brandl et al., 2016). Accordingly, conservation and restoration planning focusing on local threats are of paramount importance to improve the ecological quality of estuaries and to achieve regulatory objectives, but also to ensure functional resilience to future environmental changes (Markovic et al., 2017).

5. Conclusion

Our results have highlighted the usefulness of functional indices for determining the causal responses of fish assemblages to local disturbance more precisely than with the fish-based index (ELFI) currently used for ecological management needs of estuaries in France. Although taxonomic and functional indices were sensitive to environmental

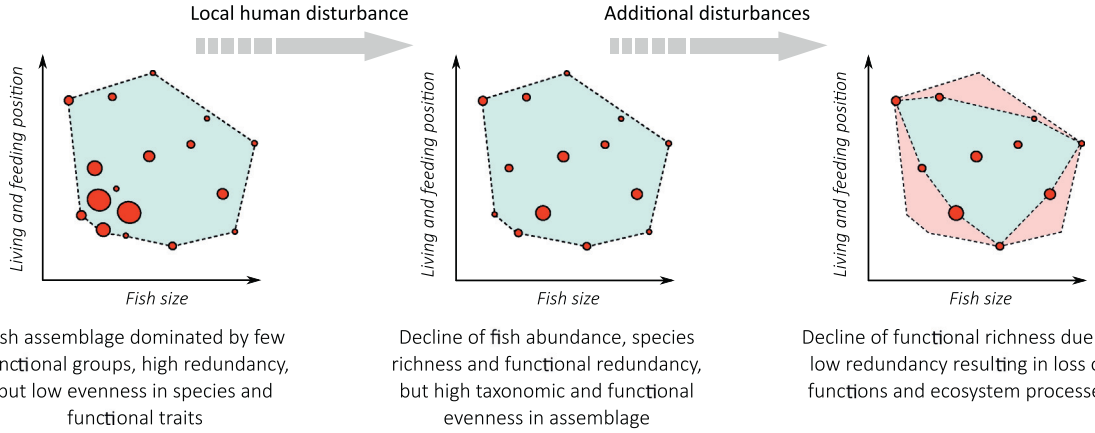
Local human disturbance
Additional disturbances
Living and feeding position
Fish size
Living and feeding position
Fish size
Living and feeding position
Fish size
Fish assemblage dominated by few functional groups, high redundancy, but low evenness in species and functional traits
Decline of fish abundance, species richness and functional redundancy, but high taxonomic and functional evenness in assemblage
Decline of functional richness due to low redundancy resulting in loss of functions and ecosystem processes

Fig. 5. Conceptual illustration of the impact of local human disturbances on taxonomic and functional structure of estuarine fish assemblages and reduction of the ability to accommodate future environmental changes. Estuarine fish assemblages are generally dominated by few functional groups and have high functional redundancy that helps to mitigate the impact of species loss. Local human disturbances lead to a decline in total abundance and species richness, but functional richness remains stable because species loss and abundance decline were mostly concentrated on dominant and redundant functional groups. However, the sharp decrease in functional redundancy when assemblages faced local disturbances makes assemblages more sensitive to additional disturbances, such as global climate change. In such a scenario, additional species loss is expected to cause decline in functional richness and alteration of ecosystem functioning.

factors (substratum composition, estuary area, depth), many of them were also responsive to local disturbances, providing opportunity to improve our mechanistic understanding of how stressors affect the structure of fish assemblages. Among other trends, our results showed that functional redundancy decreased in impacted estuaries and was more affected by human disturbance than species richness and fish abundance. This pattern was primarily influenced by the decrease of benthic fish species that were highly sensitive to anthropogenic disturbance. In consequence, monitoring of functional redundancy and benthic species can serve as early-warning indicators to identify sensitive areas where conservation efforts need to be planned.

Acknowledgements

This study was financially supported by the French Agency for Biodiversity (5 square Félix Nadar 94300 Vincennes) as part of the COPINES project. We are very grateful to the four anonymous referees for their comments and suggestions that have contributed to improve the relevance of our manuscript. We also like to thank the Adour Garonne Water Agency, Loire Bretagne Water Agency, Seine Normandie Water Agency and Artois Picardie Water Agency responsible for the fish data collection in the French estuaries.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.05.179.

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